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PHYLOGENY, EVOLUTION AND CLASSIFICATION OF MUTILLIDAE (HYMENOPTERA)

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Phylogenetic analysis of fifteen higher taxa (subfamilies and tribes) with hypothetical ancestor as outgroup reveal the relationships: Ancestor + [Myrmosinae + (Kudakrumiinae + {Pseudophotopsidinae + (Ticoplinae + [{Rhopalomutillinae + [(Ephutinae + Dasylabrinae) + Sphaeropthalminae]} + (Myrmillinae + Mutillinae)])})]. A tree generated from fifteen higher taxa and hypothetical ancestor based on 71 "best" from 89 analysed characters by PAUP yielded a length of 196 steps, CI of 0.62, RI of 0.81 and HI of 0.38. The family Mutillidae divided into ten subfamilies. The morphological evolution of Mutillidae related with loss of freely articulated pronotum and formation of mesosomal lorica in female, reduction of eye pubescense, moving of venation to the wing base, formation of RS_2 vein in forewing, strength of hamuli system of wings, formation and complication of metasomal felt lines in both sexes, shorten of gastral sternum 7 in male. Among the family the lower mutillids (Myrmosinae, Kudakrumiinae, Pseudophotopsidinae, Ticoplinae) and higher mutillids with two branches [(Myrmillinae + Mutillinae) + (Rhopalomutillinae + Dasylabrinae + Ephutinae + Sphaeropthalminae)] are separated. The classification of 224 described genera and subgenera in subfamilies and tribes is given. New classification of Ephutinae (Odontomutillini + Ephutini) and Mutillinae (Mutillini + Trogaspidiini + Petersenidiini, **stat. n.** + Smicromyrmini) is proposed.

KEY WORDS: Mutillid wasps, phylogeny, evolution, classification.

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В результате филогенетического анализа 15 высших таксонов (подсемейств и триб) и гипотетического предка, как внешней группы, выявлены следующие родственные отношения: предок + [Myrmosinae + (Kudakrumiinae + {Pseudophotopsidinae + (Ticoplinae + [{Rhopalomutillinae + [(Ephutinae + Dasylabrinae) + Sphaeropthalminae]} + (Myrmillinae + Mutillinae)])})]. Для 15 высших таксонов и гипотетического предка с помощью программы PAUP построено филогенетическое древо, основанное на 71 наиболее важном признаке из 89 проанализированных (длина = 196 шагов, CI = 0.62, RI = 0.81, HI = 0.38). Семейство Mutillidae разделено на 10 подсемейств. Морфологическая эволюция мутиллид связана с утратой подвижного пронотума и образованием мезосомального панциря у самок, редукцией опушения глаз, смещением жилкования крыльев к их основанию, появлением жилки RS_2 в переднем крыле, усилением сцепочного механизма крыла, появлением и усложнением метасомальных опушенных бороздок у обоих полов, укорочением 7-го метасомального стернума у самцов. В составе семейства выделены низшие мутиллиды (Myrmosinae, Kudakrumiinae, Pseudophotopsidinae, Ticoplinae) и высшие мутиллиды с 2 ветвями [(Myrmillinae + Mutillinae) + (Rhopalomutillinae + Dasylabrinae + Ephutinae + Sphaeropthalminae)]. Дается классификация 224 описанных родов и подродов мутиллид по подсемействам и трибам. Предложена новая классификация подсемейств Ephutinae (Odontomutillini + Ephutini) и Mutillinae (Mutillini + Trogaspidiini + Petersenidiini, **stat. n.** + Smicromyrmini).

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INTRODUCTION

The family Mutillidae includes 191 described genera (224 with subgeneric names) and 3700 described species distributed in all zoogeographical regions but predominant in tropical and subtropical regions. This family is the largest and highest among Scolioidea which includes fossil Falsiformicidae and recent Sierolomorphidae, Sapygidae, Scoliidae, Tiphiidae, Bradynobaenidae and Mutillidae (Rasnitsyn, 1980, 1988). The fossil Mutillidae are known from the Late Cretaceous (Turon, Siberia) and Eocene (Baltic amber). We used here cladistic method for the constructing of the cladogram showing phylogenetic relationships of higher mutillid taxa (subfamilies and tribes). Based on the cladograms we propose to divide Mutillidae into ten subfamilies. This paper is a part of long-term

research on phylogeny and evolution of Scolioidea of first co-author (A. Lelej) and cladistic analysis carried out by second coauthor (P. Nemkov). Second part with cladistic analysis of subfamilies and families of Scolioidea will be given separately.

SOURCES OF MATERIAL. This paper based on the richest collection of the Zoological Institute, St. Petersburg, Russia, which numbered more than 10000 mutillid specimens predominant from Central and Middle Asia collected by N. M. Przewalski, P.K. Kozlov, V.I. Roborovskij, A.P. Semenov-Tyan-Shanskij, N.A. Zarudny, L.S. Berg, A.V. Shestakov, V.V. Gussakovskij, V.V. Popov, D.M. Shteinberg. The mutillids from Zoological Museum of Moscow University (more than 2000 specimens, including A.P. Fedtschenko's collection and material collected by Soviet-Chinese expeditions in 1955-1957), Institute of Biology and Pedology, Vladivostok (more then 4000 specimens, including A.S. Lelej's collection) and Institute of Zoology, Kiev (about 1000 specimens) have been studied. A.S. Lelej collected mutillids in Middle Asia (1966-1990), Ukraine (1979), Belarus (1979, 1987), Transbaikalia (1976, 1984), Russian Far East (1973-1993), South China (1990), Japan (1991, 1993). Many colleagues (see acknowledgments) provided us with valuable exchange material from various part of the World. Valuable material has been sent for study by Sk. Yamane (from Malaysia and Indonesia) and A. Shinohara (from Japan, Taiwan and South-East Asia).

TAXA EXAMINED

Five hundreds six species from 117 genera have been studied for the receiving of morphological characters and their distribution among the fifteen higher mutilld taxa. In some cases additional data were taken after literature (see below). The list of studied genera and number of species is given herein.

MYRMOSINAE. *Carinomyrmosa* (1 sp.; ♂, ♀); *Erimyrmosa* (1 sp., ♂); *Krombeinella* (7 spp.; ♂, ♀); *Myrmosa* (5 spp.; ♂, ♀); *Paramyrmosa* (4 spp.; ♂, ♀). Additional data are taken after: Krombein (1940) and Suárez (1988).

KUDAKRUMIINAE. *Kudakrumia* (1 sp.; ♂, ♀); *Myrmosula* (1 sp.; ♂, ♀); *Protomutilla* (2 spp., ♂); *Pseudomyrmosa* (4 spp.; ♂, ♀). Additional data are taken after: Bischoff (1916) and Krombein (1979).

PSEUDOPHOTOPSIDINAE. *Pseudophotopsis* (19 spp.; ♂, ♀).

TICOPLINAE. *Areotilla* (1 sp., ♂); *Nanomutilla* (1 sp., ♀); *Smicromyrmilla* (4 spp.; ♂, ♀). Additional data are taken after: Nagy (1970) and Brothers (1975).

MYRMILLINAE. *Blakeius* (3 spp.; ♂, ♀); *Labidomilla* (2 spp., ♀); *Myrmilla* (26 spp.; ♂, ♀); *Odontotilla* (2 spp., ♀); *Platymyrmilla* (1 sp.; ♂, ♀); *Pristomutilla* (3 spp., ♀); *Sigilla* (1 sp.; ♂, ♀); *Spilomutilla* (2 spp.; ♂, ♀); *Squamulotilla* (6 spp.; ♂, ♀); *Viereckia* (1 sp., ♀).

MUTILLINAE. MUTILLINI: *Cephalotilla* (5 spp., ♂, ♀); *Ctenotilla* (3 spp.; ♂, ♀); *Mimecomutilla* (1 sp.; ♂, ♀); *Mutilla* (9 spp.; ♂, ♀); *Nanomyrme*

(2 spp., ♀); *Ronisia* (3 spp.; ♂, ♀); *Strangulotilla* (3 spp.; ♂, ♀); *Tropidotilla* (5 spp.; ♂, ♀).

SMICROMYRMINI: *Andreimyrme* (3 spp.; ♂, ♀); *Antennotilla* sp. ♂; *Corytilla* (2 spp.; ♂); *Dentilla* (13 spp.; ♂, ♀); *Ephucilla* (5 spp.; ♂); *Ephutomma* (10 spp.; ♂, ♀); *Hildebrandtia* (1 sp., ♀); *Mickelomyrme* (9 spp.; ♂, ♀); *Nemka* (13 spp.; ♂, ♀); *Nuristanilla* (1 sp., ♀); *Physetopoda* (25 spp.; ♂, ♀); *Promecilla* (3 spp.; ♂, ♀); *Psammotherma* (1 sp., ♂); *Sinotilla* (9 spp.; ♂, ♀); *Smicromyrme* (51 spp.; ♂, ♀); *Sulcotilla* (1 sp.; ♂, ♀); *Tsunekimyrme* (1 sp., ♂).

PETERSENIDIINI: *Artiotilla* (3 spp.; ♂, ♀); *Indratilla* (2 spp., ♂, ♀); *Krombeinidia* (7 spp.; ♂, ♀); *Orientidia* (3 spp.; ♂, ♀); *Pagdenidia* (1 sp., ♂); *Petersenidia* (7 spp., ♂, ♀); *Promecidia* (1 sp., ♀); *Taiwanomyrme* (1 sp., ♂); *Zavatilla* (1 sp., ♂); *Zeugomutilla* (2 spp., ♂, ♀).

TROGASPIDIINI: *Amblotropidia* (1 sp.; ♂, ♀); *Aureotilla* (1 sp.; ♂, ♀); *Carinotilla* (2 spp.; ♂, ♀); *Dentotilla* (2 spp.; ♂, ♀); *Dolichomutilla* (2 spp.; ♀); *Eotrogaspidia* (1 sp.; ♂, ♀); *Glossotilla* (3 spp.; ♂, ♀); *Lobotilla* (1 sp.; ♂, ♀); *Macromyrme* (2 spp., ♀); *Neotrogaspidia* (2 spp.; ♂, ♀); *Nonveilleridia* (1 sp., ♂); *Protrogaspidia* (1 sp., ♂); *Pseudolophotilla* (3 spp.; ♂, ♀); *Radoszkowskius* (4 spp.; ♂, ♀); *Timulla* (3 spp.; ♂, ♀); *Trispilotilla* (1 sp.; ♂, ♀); *Trogaspidia* (9 spp.; ♂, ♀).

RHOPALOMUTILLINAE: *Rhopalomutilla* (4 spp., ♂). Additional data are taken after: Bischoff (1920-1921) and Brothers (1975).

SPHAEROPTHALMINAE. PSEUDOMETHOCINI: *Atillum* (2 spp., ♀); *Darditilla* (4 spp.; ♀); *Dimorphomutilla* (1 sp., ♀); *Euspinolia* (3 spp.; ♂, ♀); *Hoplocrates* (1 sp., ♀); *Lynchiatilla* (1 sp.; ♂, ♀); *Myrmilloides* (1 sp.; ♂, ♀); *Pseudomethoca* (4 spp.; ♂, ♀); *Tallium* (7 spp.; ♂, ♀); *Vianatilla* (1 sp., ♀).

SHAEROPTHALMINI: *Acrophotopsis* (1 sp.; ♂, ♀); *Ascetotilla* (1 sp., ♀); *Australotilla* (2 spp.; ♂, ♀); *Bothriomutilla* (1 sp., ♀); *Cephalomutilla* (1 sp., ♀); *Cystomutilla* (2 spp.; ♂, ♀); *Dasymutilla* (12 spp.; ♂, ♀); *Dilophotopsis* (1 sp., ♀); *Ephutomorpha* (5 spp., ♀); *Eurymutilla* (4 spp.; ♂, ♀); *Lomachaeta* (1 sp., ♀); *Lophomutilla* (1 sp., ♀); *Micromutilla* (1 sp., ♂); *Odontophotopsis* (2 spp., ♂); *Photomorphus* (3 spp.; ♂, ♀); *Photopsis* (3 spp.; ♂, ♀); *Reedomutilla* (2 spp.; ♂, ♀); *Sphaeropthalma* (2 spp.; ♂, ♀); *Suareztilla* (1 sp., ♀); *Traumatomutilla* (5 spp.; ♀).

DASYLABRINAE: *Dasylabris* (41 spp.; ♂, ♀); *Dasylabroides* (2 spp.; ♂, ♀); *Jaxartilla* (1 sp., ♂); *Orientilla* (4 spp.; ♂, ♀); *Stenomutilla* (7 spp.; ♂, ♀); *Tricholabiodes* (9 spp.; ♂, ♀).

EPHUTINAE. EPHUTINI: Ephuta (5 spp.; ♂, ♀).

ODONTOMUTILLINI: *Odontomutilla* (8 spp.; ♂, ♀); *Odontomyrme* (1 sp., ♀); *Yamanetilla* (3 spp.; ♂, ♀).

MUTILLIDAE incertae sedis: fossil *Cretavus* (1 sp., ♂). Additional data on fossil mutillids are taken after: Rasnitsyn (1975, 1980).

CHARACTERS

The 89 following characters were used to analyze phylogenetic relationships. Their resulting matrix is given in Table 1. The hypothetical ancestor with primitive state (0) for all characters is used as outgroup. Polarity is indicated in parentheses, (0) is the primitive state, (1) is derived, (-) is polymorphic, (?) data unknown. Figures in the square brackets give the number of steps, consistency index (CI), homoplasy index (HI) and retention index (RI) correspondently of 71 "best" characters [50 double asterisked (**) most important and 21 asterisked (*) valuable ones] on the most preferred parsimonious tree (Fig. 1). 18 unasterisked characters were used for additional analyses also (Table 2). Most characters are figured in the papers (Brothers, 1975; Lelej, 1982, 1985) and not given here. The comparative names of wing venation and wing cells of Hymenoptera see: Lelej (1995a). Polarity of characters is given according their state in other Scolioidea or most primitive mutillids (Myrmosinae, Kudakrumiinae and Pseudophotopsidinae). Primitive state of third *RS* abscissa of forewing and presence of crossvein traces in forewing *1r* cell (characters 13 and 14) has been defined based on wing venation of fossil ants (Dlusskiy & Fedoseyeva, 1988). Some mutillids characters are taken from Brothers (1975) but their distribution among mutillid taxa checked throughout our material.

1. **Female ocelli: Well developed or distinguishable (0), obliterated and indistinguishable (1). [2, 0.50, 0.50, 0.67]

2. **Eye pubescence: Present (0), absent (1). [2, 0.50, 0.50, 0.75]

3. **Eye form: Flattened in profile (0), hemispherical (1). [1, 0.0, 1.0, 1.0]

4. **Male eye shape: Oval with inner margin sinuately concave (0), oval with inner margin strongly incised and emarginate (1). [3, 0.33, 0.67, 0.67].

*5. **Male antennal segment 1**: Without carina (0), with one or two carinae (1). [2, 0.50, 0.50, 0.83].

6. **Male antennal segment 3**: 1.5-2.0 times longer than antennal segment 2 (0), equal in length to second one (1).

7. **Female antennal segment 3**: 2.0 times longer than antennal segment 2 (0), equal in length to second one or 3.0 times longer of that (1).

8. **Female antennal segment 4**: 1.5-2.0 times longer than antennal segment 2 (0), equal in length to second one (1).

9. **Male antennal segment 4**: Equal in length to antennal segment 3 (0), 1.5-2.0 times longer than third one (1).

*10. **Female antennal segment 4**: Equal in length to antennal segment 3 (0), 1.5-2.0 times longer than third one (1). [3, 0.33, 0.67, 0.60].

11. **Number of maxillary and labial palpus: Six and four respectively (0), two and two respectively. [1, 1.0, 0.0, 0.0].

*12. **Forewing pterostigma**: heavily sclerotized (0), slightly sclerotized or without sclerotization (1). [3, 0.33, 0.67, 0.71].

13. **Third *RS* abscissa of forewing: With interruption (bulla) (0), without interruption (1). [2, 0.50, 0.50, 0.80].

14. **Third *RS* abscissa of forewing: With distinct angle (0), without angle (1). [1, 1.0, 0.0, 1.0].

15. ***3r-m* (second submarginal) forewing cell: Sessile anteriorly (0), petiolate anteriorly (1). [1, 1.0, 0.0, 0.0].

16. **Jugal forewing lobe: Present (0), absent (1). [1, 1.0, 0.0, 1.0].

17. **Jugal hindwing lobe: Present (0), absent (1). [1, 1.0, 0.0, 1.0].

18. **Hindwing crossvein *2r-m*: Present (0), absent (1). [2, 0.50, 0.50, 0.86]. The vein *2r-m*, which joined *RS* in apical part, presents in all Scolioidea except Bradynobaenidae and some Mutillidae and we regard such condition as plesiomorphy and absent of *2r-m* as apomorphy.

19. **Hindwing crossvein *1r-m*: Absent (0), present (1). [2, 0.50, 0.50, 0.86]. The vein *1r-m*, which joined *RS* in basal part present among Scolioidea in Bradynobaenidae and most Mutillidae and probably it is analogous of *2r-m*. We regard the absence of *1r-m*, as plesiomorphy and presence of *1r-m* as apomorphy.

*20. **Free part of hindwing *Cu* vein**: Present (0), absent (1). [3, 0.33, 0.67, 0.0]. We think that free part of hindwing *Cu* vein is plesiomorphic condition because it occurs in Thynninae and Anthoboscinae (most primitive subfamilies among Tiphiidae). To our opinion evolution of this character follows to reduction of apical part of *Cu* and crossvein *cu-a* join *M+Cu* directly.

21. **Free part of hindwing *A* vein: Present (0), absent (1). [1, 1.0, 0.0, 1.0].

*22. **Forewing *SC* vein**: With interruption (0), without interruption (1). [1, 1.0, 0.0, 1.0].

23. **Forewing RS_2 vein: Absent (0), present (1). [1, 1.0, 0.0, 1.0].

24. **Radial cell tip of forewing: Acute (0), rounded (1). [2, 0.50, 0.50, 0.80].

25. **Forewing crossvein *3r-m* and *2r-m*: Well developed (distinct) (0), less developed than other veins, indistinct or absent (1). [1, 1.0, 0.0, 1.0].

26. **Forewing crossvein *3r-m*: With interruption (0), without interruption (1). [2, 0.50, 0.50, 0.80].

27. **Forewing *1r* cell: With crossvein rudiment (0), without crossvein rudiment (1). [1, 1.0, 0.0, 1.0].

*28. **Hindwing *RS* vein**: Joined *SC* with acute angle (0), joined *SC* with rectangular angle (1). [4, 0.25, 0.75, 0.50]. We regard that join *RS* and *SC* with acute angle is plesiomorphic condition because it occurs in most Aculeata. The increasing of this angle to rectangle and more related with similar transformation in forewing.

29. **Basal hamuli: Present (0), absent (1). [1, 1.0, 0.0, 1.0].

30. **Apical hamuli: no more than 10 (0), 11-26 (1). [1, 1.0, 0.0, 1.0].

31. **First *R* abscissa of forewing**: Joined with pterostigma middle (0), joined with *SC+R* apex (1).

32. **Pterostigma**: Closed (0), open (1).

*33. **Open pterostigma**: With *SC+R* thicker than *C* (0), *SC+R* not thicker than *C* (1). [3, 0.33, 0.67, 0.50].

34. **Free part of hindwing *M* vein**: Present (0), absent (1).

35. **Hindwing crossvein *cu-a***: Present (0), absent (1).

36. **Forewing *MP* vein**: Absent (0), present (1).

37. **Notauli**: Reaching anterior scutal margin (0), equal to half of scutal length or absent (1).

38. **Axillar carina: Absent (0), present (1). [2, 0.50, 0.50, 0].

39. **Parapsids**: Absent (0), present (1).

40. **Scutal lateral ridges: Absent (0), present (1). [3, 0.33, 0.67, 0.60].

41. **Scutellar lateral carina: Absent (0), present (1). [1, 1.0, 0.0, 0.0].

42. **Scutellar medial carina or tooth: Absent (0), present (1). [1, 1.0, 0.0, 0.0].

*43. **Tegula size**: Small (0), large (1). [3, 0.33, 0.67, 0.71].

44. **Tegula length: Not protruded behind scuto-scutellar suture (0), protruded behind scuto-scutellar suture (1). [2, 0.50, 00.50, 0.50].

45. **Tegula shape: Not strongly convex, without carina (0), strongly convex, with longitudinal carina (1). [2, 0.50, 0.50, 0,0].

46. **Male metanotum: Without teeth (0), with 2 teeth (1). [1, 1.0, 0.0, 0.0].

47. **Female pronotal length: Equal to mesonotal length and more (0), 0.6 times of mesonotal length and less (1). [2, 0.50, 0.50, 0.83].

48. **Male meso-metapleural suture: Straight (0), curved forward or backward (1). [1, 1.0, 0.0, 1.0].

49. **Male meso-metapleural suture: Not curved forward (0), curved forward (1). [1, 1.0, 0.0, 1.0].

50. **Male meso-metapleural "bridge": Absent (0), present (1). [1, 1.0, 0.0, 1.0].

51. **Male oblique metapleural suture: Joined meso-metapleural suture near the middle (0), joined meso-metapleural suture in upper half (1). [1, 1.0, 0.0, 1.0].

52. **Male oblique metapleural suture: Joined meso-metapleural suture near the middle or in upper third (0), joined meso-metapleural suture in upper quarter (1). [1, 1.0, 0.0, 1.0].

*53. **Male posterior oblique episternal groove of mesopleura**: Not developed anterad of mesopleural pit (0), developed anterad of mesopleural pit (1). [1, 1.0, 0.0, 1.0].

54. **Female pro-mesonotal suture: Freely articulated (0), fused (1). [1, 1.0, 0.0, 1.0].

55. **Female mesosoma: With concave mesopleurae (0), with convex mesopleurae (1). [1, 1.0, 0.0, 1.0].

56. **Female mesopleural ridge: Weak and joined with anterior spiracle or absent (0), strong and joined with medial lateral mesonotal tubercle (1). [1, 1.0, 0.0, 1.0].

*57. **Male metasomal segment 1**: Wide and sessile anteriorly (0), narrow and petiolate anteriorly (1). [3, 0.33, 0.67, 0.0].

58. **Female meso-metapleural suture: Joined with medial lateral mesonotal tubercle (0), joined with anterior spiracle tubercle (1). [1, 1.0, 0.0, 1.0].

59. **Female meso-metapleural "bridge": Absent (0), present (1). [1, 1.0, 0.0, 1.0].

*60. **Female supracoxal mesopleural ridge**: Absent (0), present (1). [4, 0.25, 0.75, 0.40].

*61. **Female mandible**: Tridentate (0), bidentate (1). [2, 0.50, 0.50, 0.75].

* 62. **Claw**: With additional denticle (0), without denticle (1).[3, 0.33, 0.67, 0.33].

63. **Female clypeus**: With basal medial tubercle (0), without basal medial tubercle (1).

64. **Female metasomal segment 2: 0.25-0.40 times of metasomal length (0), more than 0.40 times of metasomal length (1). [1, 1.0, 0.0, 1.0].

*65. **Female metasomal segment 2**: Less than 0.55 times of metasomal length (0), more than 0.55 times of metasomal length (1). [3, 0.33, 0.67, 0.71].

66. **Felt line on metasomal segment 2 with secretory function (Debolt, 1973): Absent (0), present (1). [1, 1.0, 0.0, 1.0].

*67. **Felt line on metasomal segment 2**: Developed on tergum and sternum (0), reduced on tergum or sternum (1). [2, 0.50, 0.50, 0.75].

68. **Female scutellar scale**: Absent (0), present (1).

69. **Propodeal bend between dorsal and posterior face**: Without ridge (0), with ridge or tubercles (1).

70. **Female metasomal sternum 6: Without processes (0), with processes (1). [1, 1.0, 0.0, 0.0].

71. **Male metasomal sternum 7: No less than sternum 6 (0), remarkably less than sternum 6 (1). [1, 1.0, 0.0, 1.0].

*72. **Male metasomal sternum 7**: Not hidden under sixth sternum (0), hidden under sixth sternum (1). [3, 0.33, 0.67, 0.33].

73. **Male metasomal sternum 8 (hypopygium): Unmodified (0), trilobate (1). [1, 1.0, 0.0, 0.0].

*74. **Male unmodified hypopygium**: Without carinae or ridges (0), carinated or with processes (1). [3, 0.33, 0.67, 0.33].

75. **Male gonostylus (laterally): Short and wide (0), long and narrow (1). [1, 1.0, 0.0, 1.0].

*76. **Narrow gonostylus**: Straight (0), curved (1). [4, 0.25, 0.75, 0.57].

*77. **Narrow gonostylus**: Not curved downward (0), curved downward (1). [3, 0.33, 0.67, 0.67].

78. **Narrow gonostylus: Not curved upward (0), curved upward (1). [1, 1.0, 0.0, 1.0].

79. **Volsellar digitus: Present (0), absent (1). [2, 0.50, 0.50, 0.0].

80. **Gonostylus** (dorsoventrally): wide (0), narrow (1).

81. **Basal volsellar lobe**: Present (0), absent (1).

82. **Gonostylus dorsally**: With suture between apical and basal part (0), without suture between apical and basal part (1).

83. **Parapenial lobe of gonostylus**: Absent (0), present (1).

*84. **Relation of female propodeal length to propodeal width**: 0.5-0.7 (0), 0.3-0.4 (1). [3, 0.33, 0.67, 0.71].

*85. **Female head**: Unmodified with rounded posterolateral angles (0), enlarged with almost rectangular posterolateral angles (1). [6, 0.17, 0.83, 0.29].

86. **Pronotal pit: Absent (0), present (1). [1, 1.0, 0.0, 0.0].

87. **Lateral rounded pit on female metasomal sternum 1: Absent (0), present (1). [1, 1.0, 0.0, 0.0].

Table 1

Character matrix for 15 higher taxa of Mutillidae and 1 outgroup (hypothetical ancestor) used in cladistic analysis [**#** – most important double asterisked (**), **+** – valuable asterisked (*) in text characters]

Taxa	Characters				
	0	11	21	31	41
	####+ +	#+#######+	#+#####+##	+ # #	##+##
Ancestor	0000000000	0000000000	0000000000	0000000000	00000
Kudakrum.	10000----0	0000000000	0000001100	0000000010	00000
Myrmosinae	0000000000	0000000001	0000000100	0000000010	00000
Pseudophot.	0100000000	0000000111	10-0101101	0000010000	00000
Ticoplinae	10000---10	0111111111	1011111011	1101101000	00100
Rhopalomut.	110101??1?	1011011110	1010111011	1000001011	00101
Myrmillinae	11001010-1	0111011000	1--1111111	0100000010	00000
Odontomut.	110110-1-1	0111011110	1111111111	1111101101	10110
Dasylabrin.	11001-0010	01-1011110	1-11111011	1100101100	00100
Sphaeropth.	1110---0--	0001011110	1011111011	00000-----	00000
Pseudometh.	11100010-1	0011011110	1011111011	000000---0	00000
Mutillini	1101--10-1	0111011000	1011101111	001000-010	00110
Smicromyrm.	110110001-	0111011000	1011111111	0001000011	00100
Trogaspid.	1101101001	0111011000	1011111111	0110000011	01100
Petersenid.	1101101001	0111011000	1011111111	0110000011	00100
Ephutini	1101101100	0111011110	1111111111	1110001011	00111

Taxa	Characters				
	46	51	61	71	81
	#####	##+###+##+	++ #+#+ #	#+#+#++##	++####
Ancestor	00000	0000000000	0000000000	0000000000	000000000
Kudakrum.	00000	0000000000	1110000000	0000000001	101010000
Myrmosinae	00000	0000000000	0100000010	0010000000	001010010
Pseudophot.	10000	0001000000	0001010001	1000000001	101011110
Ticoplinae	00100	1001000001	0101010010	1001111011	101000000
Rhopalomut.	00111	10011100?0	?0?1010000	1001100011	110110000
Myrmillinae	01111	1011000011	0111010010	1001111001	111010000
Odontomut.	01111	1101110011	1111011000	110-100000	111110000
Dasylabrin.	01111	1101111010	-111111-00	1-00100000	-01100000
Sphaeropth.	01111	11-1111010	1111111-00	1100110101	111100000
Pseudometh.	01111	11-1110010	111111-000	1100110101	111110000
Mutillini	01111	10-10001-1	-111111-10	110-111001	111110000
Smicromyrm.	01111	1011000110	-1-1111110	1000111001	111100000
Trogaspid.	01111	1011000111	-1-1111--0	1001111001	1111-0001
Petersenid.	01111	1011000111	-1-1111-00	1000111001	111100000
Ephutini	01111	1101111010	1111111000	1000111001	??1000000

Remarks. Kudakrum. – Kudakrumiinae, Pseudophot. – Pseudophotopsidinae, Rhopalomut. – Rhopalomutillinae, Odontomut. – Odontomutillini, Dasylabrin. – Dasylabrinae, Sphaeropth. – Sphaeropthalmini, Pseudometh. – Pseudomethocini, Smicromyrm. – Smicromyrmini, Trogaspid. – Trogaspidiini, Petersenid. – Petersenidiini.

88. **Lateral rounded pit on male metasomal sternum 1: Absent (0), present (1). [2, 0.50, 0.50, 0.0].

89. **Male penial valvae: Symmetrical (0), asymmetrical (1). [1, 1.0, 0.0, 0.0].

CLADISTIC ANALYSIS

We made analysis with tree sets of characters using two cladistic programs. First set included only 50 double asterisked (**) most important characters and their states treated as ordered and unweighted. Second set included 71 "best" characters [50 double asterisked (**) most important and 21 asterisked (*) valuable ones] with two kinds of their states: a) the states of all 71 characters treated as ordered and unweighted, b) the states of characters treated as ordered and weighted (double asterisked = 2, asterisked = 1). Third set included 89 characters [50 double asterisked (**) most important, 21 asterisked (*) valuable and 18 unasterisked] with two kinds of their states: a) the states of all 89 characters treated as ordered and unweighted, b) the states of characters treated as ordered and weighted (double asterisked = 3, asterisked = 2, unasterisked = 1). Three data matrices showing the character state distribution for the fifteen higher taxa of Mutillidae and 1 outgroup (hypothetical ancestor) were subjected to parsimony analysis using PAUP, version 3.1 (Swofford, 1993) and Hennig86, version 1.5 (Farris, 1988). The results of cladistic analysis see in Table 2. When we used unweighted characters the trees were weakly differentiated and strikingly different from set to set in both programs. We received well differentiated similar trees when the sets of 71 and 89 weighted characters were used. The set of 89 characters yielded the same trees as Fig. 1 (for PAUP) and Fig. 2 (for Hennig86) but the length of the tree and number of reversals increased considerably (Table 2).

Table 2

The results of cladistic analysis

Cladistic program	Number of characters	Weighting	Number of trees	Consensus tree			
				Length	CI	RI	HI
Hennig86	50	no	13	70	0.71	0.83	-
Hennig86	71	no	3	127	0.55	0.73	-
Hennig86	**71**	**yes**	**1**	**196**	**0.61**	**0.77**	**-**
Hennig86	89	no	5	172	0.51	0.68	-
Hennig86	89	yes	4	371	0.56	0.73	-
PAUP	50	no	2	126	0.56	0.74	0.44
PAUP	71	no	2	128	0.56	0.73	0.44
PAUP	**71**	**yes**	**1**	**196**	**0.62**	**0.81**	**0.38**
PAUP	89	no	3	175	0.51	0.67	0.49
PAUP	89	yes	2	373	0.56	0.73	0.44

Remarks. The trees with bold data see Fig. 1 (PAUP) and Fig. 2 (Hennig86).

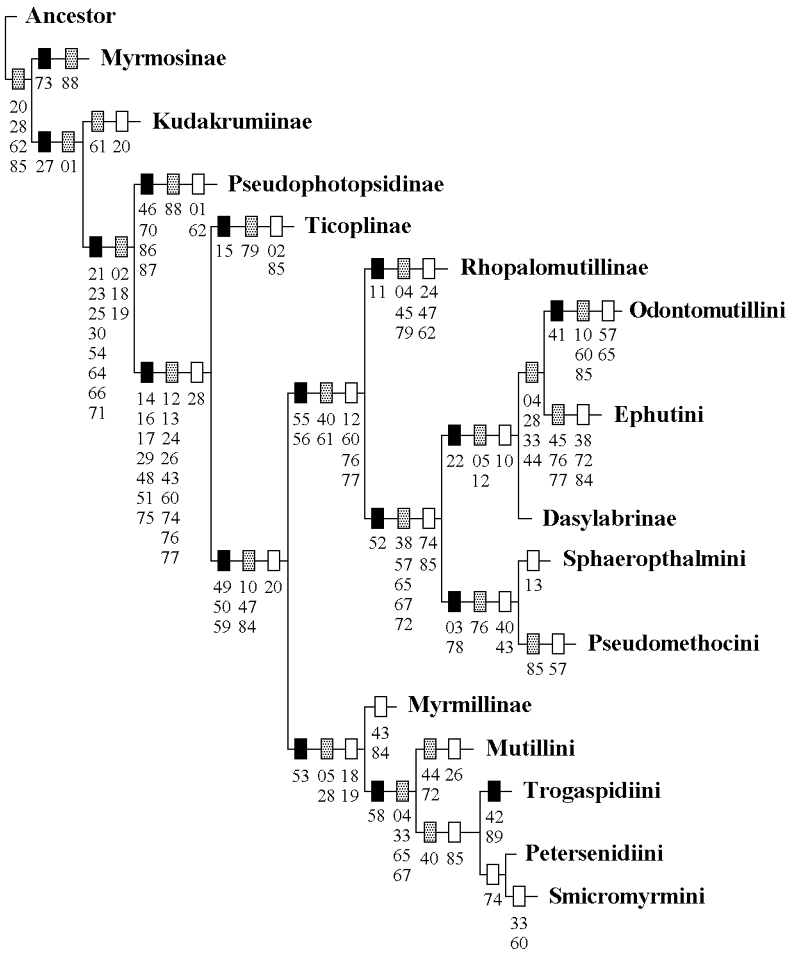


Fig. 1. Cladogram of relationships between the fifteen higher taxa of Mutillidae and Ancestor as outgroup received by program PAUP and based on 71 "best" weighted (double asterisked = 2, asterisked = 1) characters (length=196 steps, CI=0.62, RI=0.81, HI=0.38). Mutillini + Trogaspidiini + Petersenidiini + Smicromyrmini = Mutillinae; Odontomutillini + Ephutini = Ephutinae; Sphaeropthalmini + Pseudomethocini = Sphaeropthalminae. ▮ – synapomorphies or autapomorphies, ▒ – homoplasies (convergences, parallelisms), ' – reversals. The meanings of the character number and states is explained in the text.

```
    ╔═0 Ancestor
╞═29╬═2 Myrmosinae
    ║   ╔═1 Kudakrumiinae
    ╚═28╣   ╔═3 Pseudophotopsidinae
        ╚═27╣   ╔═4 Ticoplinae
            ╚═26╣                   ╔═14 Petersenidiini
                ║               ╔═17╩═12 Smicromyrmini
                ║           ╔═20╩═13 Trogaspidiini
                ║       ╔═22╩═11 Mutillini
                ║   ╔═24╩═6 Myrmillinae
                ╚═25╣   ╔═5 Rhopalomutillinae
                    ╚═23╣       ╔═10 Pseudomethocini
                        ║   ╔═19╩═9 Sphaeropthalmini
                        ╚═21╣   ╔═8 Dasylabrinae
                            ╚═18╣   ╔═7 Odontomutillini
                                ╚═16╩═15 Ephutini
```

Fig. 2. The tree derived from cladistic analysis by program Hennig86 based on 71 "best" weighted (double asterisked = 2, asterisked = 1) characters (length=196 steps, CI=0.61, RI=0.77) for the fifteen higher taxa of Mutillidae and Ancestor as outgroup. Mutillini + Trogaspidiini + Petersenidiini + Smicromyrmini = Mutillinae; Odontomutillini + Ephutini = Ephutinae; Sphaeropthalmini + Pseudomethocini = Sphaeropthalminae.

EVOLUTION

The position of lowest mutillids [Myrmosinae, Kudakrumiinae, Pseudophotopsidinae and Ticoplinae in our cladograms (Figs. 1, 2); Myrmosinae, Pseudophotopsidinae and Ticoplinae in Brothers, 1975 (Fig. 3)] is similar. But our opinion about phylogeny and evolution of higher mutillids [Rhopalomutillinae, Dasylabrinae, Ephutinae, Sphaeropthalminae, Myrmillinae and Mutillinae in our cladograms (Figs. 1, 2); Rhopalomutillinae, Myrmillinae, Mutillinae and Sphaeropthalminae in Brothers, 1975 (Fig. 3)] quite differs.

First and second divergence of mutillid steam from most primitive subfamilies Myrmosinae and Kudakrumiinae, probably, took place just after origin of Mutillidae (end of Early Cretaceous - beginning of Late Cretaceous), because *Cretavus* (Turon, Late Cretaceous), which included in Mutillidae also, had RS_2 vein, which is common for other Mutillidae beginning from Pseudophotopsidinae. The discovery of *Protomutilla* in Late Eocene (Baltic amber) not indicate the time of mutillid origin, because *Protomutilla* belongs to recent Kudakrumiinae. Subfamilies Myrmosinae and Kudakrumiinae have many symplesiomorphies that indicates their resemblance with ancestor. The main steam considerably diverge on this stage (synapomorphies 21, 23, 25, 30, 54, 64, 66, 71). The important transformations on this stage relate with loss of freely articulated pronotum and formation of mesosomal lorica in female, reduction of eye pubescense, moving of venation to the wing base, formation

of RS_2 vein in forewing, strengthening of hamuli system of wings, formation and complication of metasomal felt lines in both sexes, shortening of gastral sternum 7 in male up to hiding under sternum 6.

Third important stage, when Mutillidae diverge from Pseudophotopsidinae, associates with reduction of female ocelli, valuable changes in wing structure (loss of jugal lobe in fore- and hindwing and basal hamuli), male mesosoma (crooked meso-metapleural suture, change the position of oblique metapleural suture) and elongation of male gonostyli (synapomorphies 14, 16, 17, 29, 48, 51, 75).

Forth stage, when the higher mutillids finally diverge from the lower one (subfamily Ticoplinae), connects with formation of meso-metapleural "bridge" in both sexes and strong curving forward of male meso-metapleural suture (synapomorphies 49, 50, 59).

After that higher mutillids diverged in two branches (Myrmillinae + Mutillinae) and (Rhopalomutillinae + Dasylabrinae + Ephutinae + Sphaeropthalminae). The first branch of higher mutillids (Myrmillinae + Mutillinae) conserved female mesosoma with concave mesopleurae and propodeum wider than mesonotum (characteristic of lower Pseudophotopsidinae) but notal sutures became indistinct and pronotum became much shorter. The main evolution tendency in this branch became the male wingless (some Myrmillinae) and development of phoretic copulation (mating last until one hour in Mutillinae, see: Crevecoeur, 1930; Linsley, 1960; Sheldon, 1970; Alicata et al., 1975). We think that reversals 18, 19 connect with strengthening of flight, that it is important for phoresy. Myrmillinae, which has not synapomorphies in this branch, probably, is ancestor for Mutillinae and evolution of the latter connected with changing of male eye shape (inner margin strongly incised and

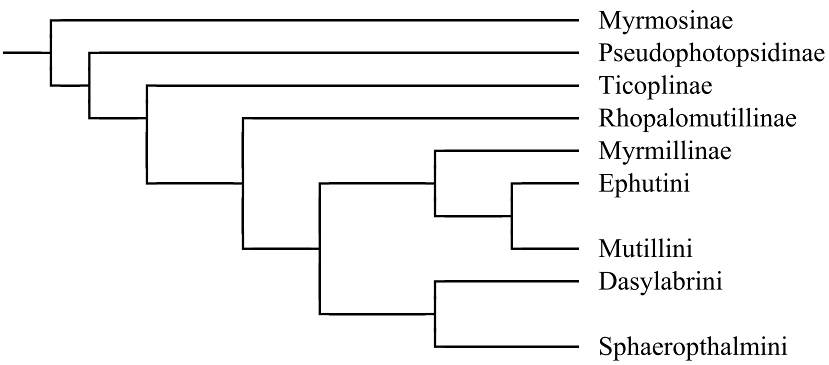


Fig. 3. Cladogram of relationships of nine higher taxa of Mutillidae, based on 43 "best" characters, after Brothers (1975). Mutillini (Mutillina + Smicromyrmina) + Ephutini = Mutillinae; Dasylabrini + Sphaeropthalmini (Pseudomethocina + Sphaeropthalmina) = Sphaeropthalminae.

emarginate), elongation of tegulae and formation of scutal lateral ridges (apomorphies 4, 44 and 40). But latter occurs in the second branch of higher mutillids also. Among the Mutillinae tribe Trogaspidiini has medial scutellar ridge or tubercle and asymmetrical penial valvae (strong autapomorphies among Mutillidae) and distinctly differs from Mutillini, Petersenidiini and Smicromyrmini which have homoplasies and reversals only.

The second branch of higher mutillids (Rhopalomutillinae + Dasylabrinae + Ephutinae + Sphaeropthalminae) connects with considerable change of female mesosoma which become convex with mesonotum much wider than propodeum (synapomorphies 55, 56). The differentiation of mesosomal segments in this branch lead to further increasing and domination of mesothorax. The male scutal lateral ridges characteristic of this branch occur in Mutillinae also (homoplasy 40). The main evolution tendency in this branch became the shortening of copulation. In more primitive Rhopalomutillinae mating lasts long time, likes Mutillinae (Brothers, 1972), in advanced Dasylabrinae and Sphaeropthalminae this time is 5-20 seconds only (Brothers, 1972; Baylis & Brothers, 1996). Sphaeropthalminae + Dasylabrinae + Ephutinae diverge considerably (synapomorphy 52, homoplasies 38, 57, 65, 67, 72) from more primitive Rhopalomutillinae. Then Sphaeropthalminae which has subcircular eyes and very narrow curved up gonostyli (autapomorphies 3, 78) separated from Dasylabrinae + Ephutinae. Dasylabrinae which has not synapomorphies, probably, is ancestor for Ephutinae and evolution of the latter connected with changing of male eye shape (inner margin strongly incised and emarginate) and elongation of tegulae (apomorphies 4, 44). Relation between Dasylabrinae and Ephutinae is similar to that of Myrmillinae and Mutillinae in the first branch of higher mutillids. Among Ephutinae Odontomutillini has scutellar lateral ridge (autapomorphy among Mutillidae) and homoplasies 10, 60, 85 and remarkably differs from Ephutini.

CLASSIFICATION

The composition of family Mutillidae and number of included subfamilies are changed for a long time. The eight current subfamilies (Pseudophotopsidinae, Ticoplinae, Rhopalomutillinae, Myrmillinae, Mutillinae, Dasylabrinae, Ephutinae and Sphaeropthalminae) were including in Mutillidae without doubtful, but their status were changing. The including of Myrmosinae, Kudakrumiinae, Typhoctinae, Chyphotinae and Apterogyninae was always problematic.

Primery subfamilies Chyphotinae and Apterogyninae have been included in Mutillidae (André, 1903) or Myrmosidae (Ashmead, 1903) and later separated in family Apterogynidae (Invrea, 1957). Both subfamilies belong now to Bradynobaenidae (Brothers, 1975; Nonveiller, 1990; Genise, 1986; Rasnitsyn, 1980, 1988; Brothers & Finnamore, 1993).

Subfamilies Typhoctinae and Eotillinae were included in Mutillidae (Krombein & Schuster, 1957; Mickel, 1967; Krombein, 1979a;), but later their

status reduce to tribal level among subfamily Typhoctinae in Bradynobaenidae (Brothers, 1975). Our attempt to prove the subfamily Typhoctinae among Mutillidae based on many morphological characters was unsuccessful and we received the same result as Brothers (1975). Such synapomorphies as paired stridulitra on metasomal tergum 4, strong reduction of metasomal tergum 1 and gonapophysis VIII of female without basal valve definitely unite Typhoctinae with Bradynobaenidae where it placed near the base of tree.

Subfamily Kudakrumiinae has been proposed by Krombein (1979b) for two Oriental genera *Kudakrumia* Krombein and *Nothomyrmosa* Krombein among Mutillidae. Later it was placed as subfamily in Myrmosidae (Suárez, 1988) or as tribe in Myrmosinae (Brothers & Finnamore, 1993). We included in Kudakrumiinae Palaearctic *Pseudomyrmosa* Suárez, Nearctic *Myrmosula* Bradley and *Leiomyrmosa* Wasbauer and fossil *Protomutilla* Bischoff (from Eocene of Baltic amber) and regarded it as intermediate link between Myrmosinae and other Mutillidae (Lelej, 1981, 1986). These small wasps similar to Myrmosinae by male venation, freely articulated female pro-mesonotal suture, lacking lateral felt lines on metasomal segment 2 in both sexes, but resemble with other Mutillidae by genitalia structure and hypopygium shape in male, by lacking ocelli and basal clypeal tubercle in female. In spite of that Kudakrumiinae has such apomorphies as male forewing without developed jugal lobe, reduced female ocelli, but lacking lateral felt lines on metasomal segment 2, eye pubescence and weak stridulitra in both sexes, weakly or unmodified hypopygium and venation extending to apical wing margin in male, freely articulated pronotum and wide long metasomal segment 1 in female relate Kudakrumiinae with hypothetical ancestor of Mutillidae.

Subfamily Myrmosinae has been separated as a tribe among Mutillidae (Fox, 1894). Later Ashmead (1899) united genera *Myrmosa*, *Brachycistis*, *Bradynobaenus* and *Chyphotes* in distinct family Myrmosidae and André (1903) regarded Myrmosinae among Mutillidae. At the same time Ashmead (1903) divided Myrmosidae into three subfamilies: Bradynobaeninae, Myrmosinae (including tribes Myrmosini and Chyphotini) and Apterogyninae. Original composition of Myrmosidae has been proposed by Skorikov (1927, 1935), who included in this family three subfamilies: Myrmosinae (*Myrmosa*), Myrmillinae (*Myrmilla*) and Pseudophotopsidinae (*Pseudophotopsis*). The latter was known in those times upon male only. Beginning from Krombein (1940) current composition of Myrmosinae has been accepted and it was placed in Tiphiidae (Pate, 1947; Wasbauer, 1973; Krombein, 1979a). Some taxonomists, especially who study Mutillidae, prefered to regard Myrmosidae as distinct family (Invrea, 1952, 1964; Suárez, 1960, 1963; Lelej, 1977, 1978). Based on morphological analysis of Aculeata Brothers (1975) placed Myrmosinae in Mutillidae. It was accepted by Lelej (1985) also. Such synapomorphy as well developed trilobate (sometimes with two additional processes) hypopygium (autapomorphy among Scolioidea) divide considerably Myrmosinae from other Mutillidae which has unmodified hypopygium. The

beginning of hypopygium differentiation into medial part and lateral projections discovered in *Kukakrumia mirabilis* Krombein (Kudakrumiinae). Brothers (1974) thought even that *Nothomyrmosa microsoma* (Brothers) belongs to fossil *Protomutilla* that stress primitive characters of Kudakrumiinae. The distribution of Myrmosinae resembles that of Kudakrumiinae: Palaearctic *Carinomyrmosa, Krombeinella, Paramyrmosa*, Nearctic *Myrmosina*; *Myrmosa* distributed in Palaearctic (four species), Nearctic (four species) and Oriental region (one doubtful species from Java), *Erimyrmosa* includes one Palaearctic and one Oriental species.

Such symplesiomorphies of Myrmosinae and Kudakrumiinae as freely articulated pronotum and lacking basolateral processes on metasomal tergum 1 in female, venation extending to apical margin in fore- and hindwing and lacking RS_2 vein in male, show the primitivity of both subfamilies and their relation with hypothetical ancestor of Mutillidae. As regards the life history of both subfamilies, the hosts are known for Nearctic *Myrmosula parvula* (Fox) - parasite of *Lasioglossum zephyrum* (Smith) (Halictidae) (Brothers, 1978), Palaearctic *Myrmosa atra* F. - *Oxybelus uniglumis* L. (Sphecidae) (Giner, 1944), Nearctic *M. unicolor* Say - *Tiphia* sp. (Tiphiidae), *Lindenius columbianus errans* (Fox) (Sphecidae), *Dialictus pruinosus* (Robt.), *D. inconspicuus* (Smith) (Halictidae) (Krombein, 1979a). Probably the other species of Myrmosinae and Kudakrumiinae can parasite on pupae and prepupae of Aculeata. Some morphological characters relate both subfamilies with family Tiphiidae and Bradynobaenidae, but the life history similar to that of Mutillidae for those the parasiting on immature Aculeata was main evolution trend.

Based on phylogenetic research and evolution of Mutillidae we proposed here family classification, which differs considerably in some branches from that, proposed by Brothers (1975). The main differences are the resurrection of subfamily Ephutinae (Ephutini + Odontomutillini) and subfamily Dasylabrinae and the tribal differentiation in Mutillinae (Mutillini + Trogaspidiini + Petersenidiini + Smicromyrmini).

We include in our system all valid genera (190) and subgenera (33) described in various catalogues, monographs and revisions (Ashmead, 1900-1904; André, 1899-1903a, 1903b; Bischoff, 1920-1921; Chen, 1957; Brothers, 1975, 1994; Krombein, 1979a; Nonveiller, 1973, 1977, 1980a, 1980b, 1990, 1993, 1995a, 1995b, 1995c, 1995d, 1996; Nonveiller et Cetkovic, 1996; Lelej, 1995b, 1995c, 1996; Quintero & Cambra, 1996). Synonyms are given in the round brackets with symbol "=", valid subgeneric names are given in the square brackets. The genera are numbered in alphabetical order within tribe or subfamily.

Family MUTILLIDAE Latreille, 1802

1. Subfamily MYRMOSINAE Fox, 1894

Carinomyrmosa Lelej, 1981;
Erimyrmosa Lelej, 1984;
Krombeinella Pate, 1947
(=***Paramyrmosa*** Suárez, 1983);
Myrmosa Latreille, 1796
(=***Ischioceras*** Provancher, 1882);
Myrmosina Krombein, 1940;
Paramyrmosa Saussure, 1880
(=***Morysmula*** Suárez, 1963).

2. Subfamily KUDAKRUMIINAE Krombein, 1979

Kudakrumia Krombein, 1979;
Leiomyrmosa Wasbauer, 1963;
Myrmosula Bradley, 1917;
Nothomyrmosa Krombein, 1979;
Protomutilla Bischoff, 1916;
Pseudomyrmosa Suárez, 1980.

3. Subfamily PSEUDOPHOTOPSIDINAE Bischoff, 1920

Pseudophotopsis André, 1896
(=***Alloneurion***, Ashmead, 1899;
Sphinctomutilla André, 1903).

4. Subfamily TICOPLINAE Nagy, 1970 (=Nanomutillinae Suárez, 1975)

Tribe TICOPLINI Nagy, 1970

Areotilla Bischoff, 1920;
Nanomutilla André, 1900;
Ticopla Nagy, 1970.

Tribe SMICROMYRMILLINI Argaman, 1988

Smicromyrmilla Suárez, 1965.

5. Subfamily MYRMILLINAE Bischoff, 1920

Blakeius Ashmead, 1903
(=***Bisigilla*** Skorikov, 1927);
Ceratotilla Bischoff, 1920;
Clinotilla Arnold, 1956;
Labidomilla André, 1903;
Liomutilla André, 1907;
Liotilla Bischoff, 1920;
Myrmilla Wesmael, 1851
(=***Rudia*** Costa, 1858)
[***Eurygnathilla*** Skorikov, 1927;
Pseudomutilla Costa, 1885
(=***Edrionotus*** Radoszkowski, 1850];
Myrmotilla Bischoff, 1920;
Omotilla Invrea, 1943;
Platymyrmilla André, 1900;
Pygomilla Hammer, 1955;
Odontotilla Bischoff, 1920
[***Arnoldtilla*** Nonveiller, 1996;
Botswanotilla Nonveiller, 1996;
Cataractaetilla Nonveiller, 1996;
Conjunctotilla Nonveiller, 1996;
Odontilloides Nonveiller, 1996;
Saganotilla Invrea, 1943];
Pristomutilla Ashmead, 1903
[***Acanthomutilla*** Nonveiller, 1995;
Diacanthotilla Nonveiller, 1995];
Sigilla Skorikov, 1927;
Somaliatilla Nonveiller, 1995;
Spilomutilla Ashmead, 1903;
Squamulotilla Bischoff, 1920;
Viereckia Ashmead, 1903.

6. Subfamily MUTILLINAE Latreille, 1802

Tribe MUTILLINI Latreille, 1802

Barymutilla André, 1901;
Cephalotilla Bischoff, 1920
[***Bidentotilla*** Nonveiller, 1978;
Taeniotilla Nonveiller, 1978];
Chaetomutilla Nonveiller, 1978;
Ctenotilla Bischoff, 1920;
Hadrotilla Bischoff, 1920;
Mimecomutilla Ashmead, 1903;
Montanomutilla Nonveiller, 1978;
Mutilla Linnaeus, 1756;
Nanomyrme Lelej, 1977;
Pseudocephalotilla Bischoff, 1920;

Ronisia Costa, 1858
(=***Pycnotilla*** Bischoff, 1920);
Seriatospidia Nonveiller et Cetkovic, 1996;
Spinulotilla Bischoff, 1920;
Strangulotilla Nonveiller, 1978;
Tropidotilla Bischoff, 1920.

Tribe SMICROMYRMINI Bischoff, 1920

Andreimyrme Lelej, 1995;
Antennotilla Bischoff, 1920;
Bisulcotilla Bischoff, 1920;
Corytilla Arnold, 1956;
Ctenoceraea Nonveiller, 1993;
Dentilla Lelej, 1980;
Ephucilla Lelej, 1995;
Ephutomma Ashmead, 1899
(=***Eremomyrme***, Suárez, 1965);
Guineomutilla Suárez, 1977;
Gynandrotilla Arnold, 1946;
Hildebrandtia Olsoufieff, 1938;
Mickelomyrme Lelej, 1995;
Nuristanilla Lelej, 1980;
Nemka Lelej, 1986
(=***Horaia*** Tsuneki, 1993);
Physetopoda Schuster, 1949
(=***Paramyrme*** Lelej, 1977);
Promecilla André, 1903;
Psammotherma Latreille, 1802;
Sinotilla Lelej, 1995;
Smicromyrme Thomson, 1870
[***Astomyrme*** Schwartz,1984;
Eremotilla Lelej, 1986;
Erimyrme Lelej, 1986;
Rhombotilla Nagy, 1966];
Sulcotilla Bischoff, 1920;
Tsunekimyrme Lelej, 1995.

Tribe PETERSENIDIINI Lelej, 1996, **stat. n.**

Artiotilla Invrea, 1950
(=***Glossomyrme***, Suárez, 1979);
Indratilla Lelej, 1993;
Krombeinidia Lelej, 1996;
Orientidia Lelej, 1996;
Pagdenidia Lelej, 1996;
Peringueyella Nonveiller, 1995;
Petersenidia Lelej, 1992;
Promecidia Lelej, 1996;
Taiwanomyrme Tsuneki, 1993;
Zavatilla Tsuneki, 1993;
Zeugomutilla Chen, 1957.

Tribe TROGASPIDIINI Bischoff, 1920

Amblotropidia Nonveiller, 1995;
Aureotilla Bischoff, 1920;
Carinotilla Nonveiller, 1973;
Chrysotilla Bischoff, 1920;
Curvitropidia Nonveiller, 1995;
Dentotilla Nonveiller, 1977;
Dolichomutilla Ashmead, 1899;
Eotrogaspidia Lelej, 1996;
Glossotilla Bischoff, 1920;
Lobotilla Bischoff, 1920;
Lophotilla Bischoff, 1920;
Macromyrme Lelej, 1984;
Neotrogaspidia Lelej, 1996;
Nonveilleridia Lelej, 1996;
Protrogaspidia Lelej, 1996;
Pseudolophotilla Nonveiller, 1995;
Radoszkowskius Ashmead, 1903;
Timulla Ashmead, 1899;
Trispilotilla Bischoff, 1920;
Trogaspidia Ashmead, 1899
[***Acutitropidia*** Nonveiller, 1995;
Arcuatotropidia Nonveiller, 1995;
Chilotropidia Nonveiller, 1995;
Inflatispidia Nonveiller, 1995;
Lobotropidia Nonveiller, 1995];
Tuberocoxotilla Nonveiller, 1980.

MUTILLINAE incertae sedis: ***Sylvotilla*** Olsoufieff, 1938.

7. Subfamily RHOPALOMUTILLINAE Schuster, 1949

Rhopalomutilla André, 1901.

8. Subfamily SPHAEROPTHALMINAE Schuster, 1949(1903) (=Cystomutillinae Invrea,1964)

Tribe PSEUDOMETHOCINI Schuster, 1947

Allotilla Schuster, 1949;
Ancipitotilla Mickel, 1952;
Anomophotopsis Schuster, 1949;
Atillum André, 1903;
Calomutilla Mickel, 1952;
Chaetotilla Schuster, 1949;
Darditilla Casal, 1965;
Dimorphomutilla Ashmead, 1903;
Euspinolia Ashmead, 1903
(=***Reedia*** Ashmead, 1904);
Gurisita Casal, 1970;
Hoplocrates Mickel, 1937
(=***Hoplomutilla*** André, 1903);
Hoplognathoca Suárez, 1962;
Hoplomutilla Ashmead, 1899
(=***Tilluma*** André, 1903);
Horcomutilla Casal, 1962;
Invreiella Suárez, 1966;
Jamaitilla Casal, 1965;
Lynchiatilla Casal, 1963;
Mammomutilla Mickel, 1952;
Mickelia Suárez, 1966;
Myrmilloides André, 1903;
Pappognatha Mickel, 1939;
Patquiatilla Casal, 1962;
Pertyella Mickel, 1952;
Pseudomethoca Ashmead, 1896
(=***Nomiephagus*** Ashmead, 1899);
Seabratilla Casal, 1963;
Sphinctopsis Mickel, 1928
(=***Sphinctomutilla*** André, 1909);
Tallium André, 1903;
Vianatilla Casal, 1962.

Tribe SPHAEROPTHALMINI Schuster, 1949(1903)

Acanthophotopsis Schuster, 1958;
Acrophotopsis Schuster, 1958;
Ascetotilla Brothers, 1971;
Australotilla Lelej, 1983;
Bordontilla Fritz et Martinez, 1975;
Bothriomutilla Ashmead, 1899;
Cephalomutilla André, 1908;
Ceratophotopsis Schuster, 1949;
Cystomutilla André, 1896;
Dasymutilla Ashmead, 1899
(=***Bruesia*** Ashmead, 1903;
=***Pycnomutilla*** Ashmead, 1903);
Dilophotopsis Schuster, 1958;
Ephutomorpha André, 1903;
Eurymutilla Ashmead, 1899;
Huacotilla Casal, 1962;
Leucospilomutilla Ashmead, 1903;
Limaytilla Casal, 1964;
Lomachaeta Mickel, 1936;
Lophomutilla Mickel, 1952
(=***Paramutilla*** Mickel, 1973);
Lophostigma Mickel, 1952;
Morsyma Fox, 1899;
Nanotopsis Schuster, 1949
(=***Chasquitilla*** Casal, 1970);
Neomutilla Reed, 1898;
Odontophotopsis Viereck, 1903
(=***Tetraphotopsis*** Ashmead, 1903);
Periphotopsis Schuster, 1958;
Photomorphus Viereck, 1903
[***Photomorphina*** Schuster, 1952
(=***Photomorphina*** Schuster, 1958);
Xenomorphus Schuster, 1958];
Photopsis Blake, 1886
(=***Agama*** Blake, 1871;
=***Pyrrhomutilla*** Ashmead, 1899;
=***Neophotopsis*** Ashmead, 1903);
Physetapsis Schuster, 1958;

Ponerotilla Brothers, 1994;
Protophotopsis Schuster,1946
[***Protophotopsiella*** Schuster,1949];
Ptilomutilla André, 1905;
Reedomutilla Mickel, 1964
(=***Reedia*** André, 1904);
Scaptodactyla Burmeister, 1875;
Scaptopoda F.Lynch-Arribalzaga, 1878;
Smicromutilla Mickel, 1964;
Sphaeropthalma Blake, 1871
(=***Sphaerophthalma*** Blake, 1886)
[***Micromutilla*** Ashmead, 1899;
Photopsioides Schuster, 1958;
Xenophotopsis Schuster, 1958];
Suareztilla Casal, 1968;
Tobantilla Casal, 1964;
Traumatomutilla André, 1901;
Xystromutilla André, 1905.

9. Subfamily DASYLABRINAE Skorikov, 1935

Apteromutilla Ashmead, 1903
(=***Apterotilla*** Bischoff, 1920);
Brachymutilla André, 1901;
Dasylabris Radoszkowski, 1885
(=***Allomutilla*** Ashmead, 1899)
[***Baltilla*** Lelej, 1976;
Craspedopyga Lelej, 1976;
Inbaltilla Lelej, 1976];
Chrestomutilla Brothers, 1971;
Dasylabroides André, 1901;
Jaxartilla Lelej, 1984;
Orientilla Lelej, 1979;
Stenomutilla André, 1896
[***Seyrigilla*** Krombein, 1972];
Tricholabiodes Radoszkowski, 1885;
Xenomutilla Ashmead, 1903.

10. Subfamily EPHUTINAE Ashmead, 1903

Tribe EPHUTINI Ashmead, 1903

Ephuamelia Casal, 1968;
Ephuchaya Casal, 1968;
Ephusuarezia Casal, 1968;
Xenochile Schuster, 1957;
Ephuta Say, 1836
(=***Rhoptromutilla*** André, 1903)
[***Ephuseabra*** Casal, 1968;
Ephutopsis Ashmead, 1904
(=***Arcasina*** Nagy, 1970);].

Tribe ODONTOMUTILLINI Lelej, 1983

Odontomutilla Ashmead, 1899
(=***Peringueya*** Ashmead, 1903);
Odontomyrme Lelej, 1983;
Yamanetilla Lelej, 1996.

MUTILLIDAE incertae sedis: ***Cretavus*** Sharov, 1957.

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